

Dermatoglyphic Variation in Europe

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ABSTRACT We describe the geographic variation patterns of 236 dermatoglyphic variables (118 for each sex) for 74 samples in Europe. Using principal components analysis and rotating to simple structure, we simplified these patterns to the first 20 axes, representing 74.2% of covariation. We then used heterogeneity tests, interpolated surfaces, one-dimensional and directional correlograms, and distances between correlograms to analyze the factor scores of these 20 axes. We also ordinated the 74 localities. The data are remarkable for showing little spatial autocorrelation, despite significant heterogeneity among localities. Only three factor axes exhibit consistently significant correlograms, indicating that there are few spatial patterns in the original variables in Europe. Almost all correlations between pairs of variables occur within serially homologous character sets and are thus developmentally determined. There is some support for demic diffusion from the southeast in finger patterns and ridge counts. We compare these results to those of previous studies and note that Lapps and Icelanders are outliers with respect to both genetics and finger tip variables, whereas Tatars are outliers with respect to craniometrics and dermatoglyphics. © 1996 Wiley-Liss, Inc.

In recent years, members of the Stony Brook Human Variation Laboratory have studied the geographic variation of physical anthropological variables in Europe, specifically, craniometric variables (Sokal and Uytterschaut, 1987) and blood polymorphisms (Sokal et al., 1989). The aim of these studies was not only to describe the major patterns of variation over the continent, but also to infer historical and demographic forces that have led to the patterns. Sokal et al. (1989), in their spatial analysis of blood polymorphisms, concluded that the variation among the surfaces of these genetic markers could be summarized by a few major patterns. They inferred the following population models: isolation by distance, ethnic settlement, Neolithic transition by demic expansion, and latitudinal selection. Harding (1990) com-

pared the results for the blood polymorphisms to those for cranial variation and found that both sets of results could be accounted for by the same, or similar, population processes.

In this study we analyze a set of European samples, measured for dermatoglyphic variables. This is the most extensive study of European dermatoglyphics, in terms of the number of European localities, as well as the number of variables, that has been undertaken to date. In the Discussion section, we compare the findings from this study to those

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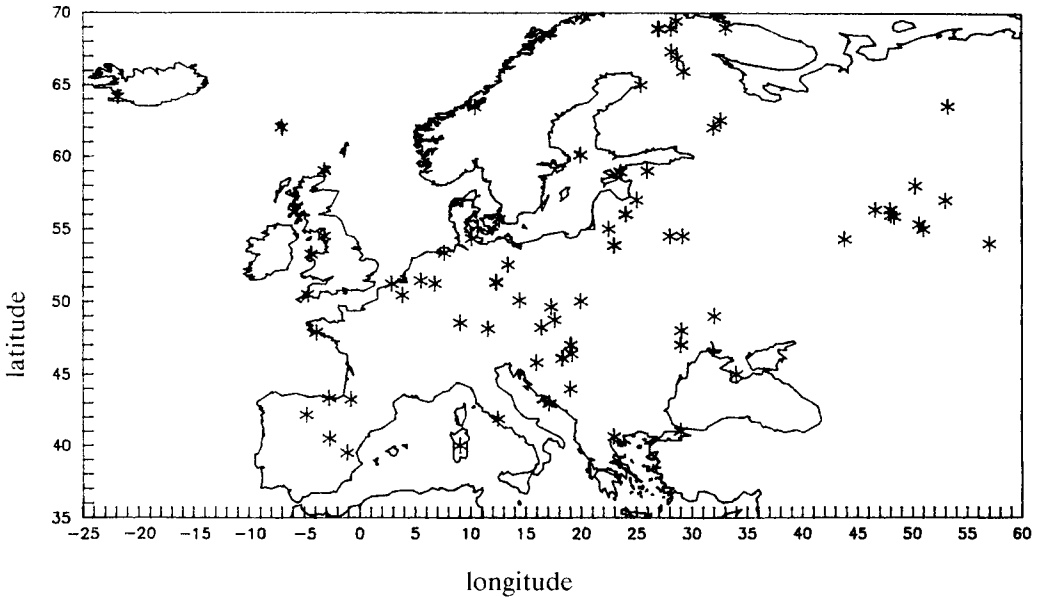


Fig. 1. The 74 localities in Europe analyzed in this study. The axes are degrees longitude and latitude.

of the earlier ones on craniometric variables and blood polymorphisms.

MATERIALS AND METHODS

The European dermatoglyphics dataset consists of samples at 74 localities distributed widely over Europe (see Fig. 1). The data comprise variant frequencies and mean ridge counts for both males and females. Sample sizes range from a low of 19 to a high of 519. These data originate from a world dermatoglyphic data base assembled by the late Heinz Brehme, Freiburg University, and R.L. Jantz. Several samples originate from Brehme's own collection, but most are samples collected by others. However, all of the prints were made available to Brehme for analysis. He carried out all of the ridge-counting and pattern classification, eliminating interobserver variation. Appendix A lists the samples, geographic coordinates, and the original investigators.

The variables measured are described in Jantz et al. (1992). They consist of 32 finger patterns (16 each of the right and left digits), 22 palm patterns (11 for each hand), and 38 mainline terminations (19 for each hand). These categorical variables are given as fre-

quencies of the pattern types and are stated as proportions analogous to allele frequencies. In addition, there are 20 finger-ridge counts and six palm-ridge counts. For these meristic variables we employed mean counts per locality. For each locality, therefore, we had a total of 236 (118 for each sex) variant frequencies or mean-ridge counts.

We tested for the presence of heterogeneity among localities by analyses of variance for mean-ridge counts and *G*-tests for homogeneity for the variant frequencies. Both methods are described in Sokal and Rohlf (1995).

Because of the serial homology of many of the variables describing patterns for different fingers, there was a good deal of correlation among the 236 variables. To reduce this correlation and simplify the spatial analyses, we carried out a principal components analysis that extracted the first 20 orthogonal factors representing 74.2% of the covariation. It was possible to do this with these data since they were completely balanced, with no missing values. We rotated the principal axis loadings orthogonally by the varimax criterion (PROC FACTOR; SAS) and computed factor scores for the 74 localities on the 20 axes.

The analysis consisted of mapping and contouring the factor scores using the SURFER program (Golden Software). This afforded us a visual representation of dermatoglyphic variation in space.

To test for spatial structure in the factor scores, we subjected scores for each of the 20 factors to a spatial autocorrelation analysis, testing for positive or negative spatial association of these scores with distance. We used both Moran's *I*, a product-moment coefficient, and Geary's *c*, a distance-like coefficient (Sokal and Oden, 1978a,b; Cliff and Ord, 1981; Upton and Fingleton, 1985). The rather involved relations between the two coefficients are discussed in Sokal (1979). Moran's *I* is the more frequently employed of the two coefficients, perhaps because of its similarity to the widely used Pearson product-moment coefficient. However, contrary to our experience with other datasets, Geary's *c* yielded the stronger autocorrelation patterns. We computed one-dimensional correlograms (Sokal and Oden, 1978a,b; Upton and Fingleton, 1985) for ten distance classes, calculating geographic distance between the localities as great circle distances. The ten distance classes had upper limits of 575, 875, 1,125, 1,350, 1,600, 1,800, 2,100, 2,425, 2,825, and 4,425 km, respectively. The plot of the autocorrelation coefficients against distance is referred to as a correlogram (see Fig. 2 below), the overall significance of which is assessed through a Bonferroni test (Oden, 1984).

Directional spatial correlograms permit the separation of clinical trends in different compass directions (Oden and Sokal, 1986). We resolved the linear or one-dimensional correlograms in two-dimensional space as directional spatial correlograms. By this method, Moran's *I* and Geary's *c* autocorrelation coefficients were computed for classes based not only on the distance between pairs of localities, but also on the mutual compass bearing of each pair of points. We chose five distance classes with upper limits of 220, 780, 1,680, 2,920, and 4,500 km, respectively. Although directional correlograms are radially symmetric, we show sample correlograms (see Fig. 3 below) as complete circular sets of coefficients for ease of interpretation. Again we used Bonferroni tests to

determine the overall significance of these correlograms.

To identify the number of independent variational trends, we estimated similarities of both Bonferroni-significant one-dimensional and directional correlograms by computing average Manhattan distance between pairs of correlograms over the distance classes (Sneath and Sokal, 1973). We then clustered these distances with a nonhierarchical clustering method (*k*-means clustering; Späth, 1980) that finds the minimum pooled sum of squares within groups for a partition of *N* items, in *k* groups, by means of a hill-climbing algorithm. The final clustering was the minimum solution over 100 trials, with random initial starting positions. We repeated this procedure for *k* = 2 through 10 classes and determined the number of clusters by examining the slope of the curve of sums of squares, plotted against *k*. In these data, unlike previous studies, only two, or at most three, clusters were evident.

The procedures of spatial autocorrelation analysis enumerated above have been described by Sokal and Oden (1978a,b), and inferential procedures based on them were developed by Sokal (1979), Sokal and Warntenberg (1981), and Sokal (1984, 1986).

RESULTS

G-tests of the variant frequencies and analyses of variance of the ridge counts indicated high nominal significance for heterogeneity in all 236 tested variables. Typically the significance of spatially distributed variables is exaggerated by the presence of spatial autocorrelation in the variables. As there was remarkably little spatial autocorrelation in this dataset (see below), we can conclude with considerable assurance that the spatial differentiation of the observed variables is real. There appear to be significant differences in these dermatoglyphic variables among the populations tested.

Table 1 presents the descriptions of the 20 factors we analyzed. It gives the dominant variables contributing to each factor, defined as loadings greater than 0.5. The original variables fall into five categories: 1) finger patterns; 2) finger ridge counts; 3) palm ridge counts; 4) palm patterns; and 5) palm

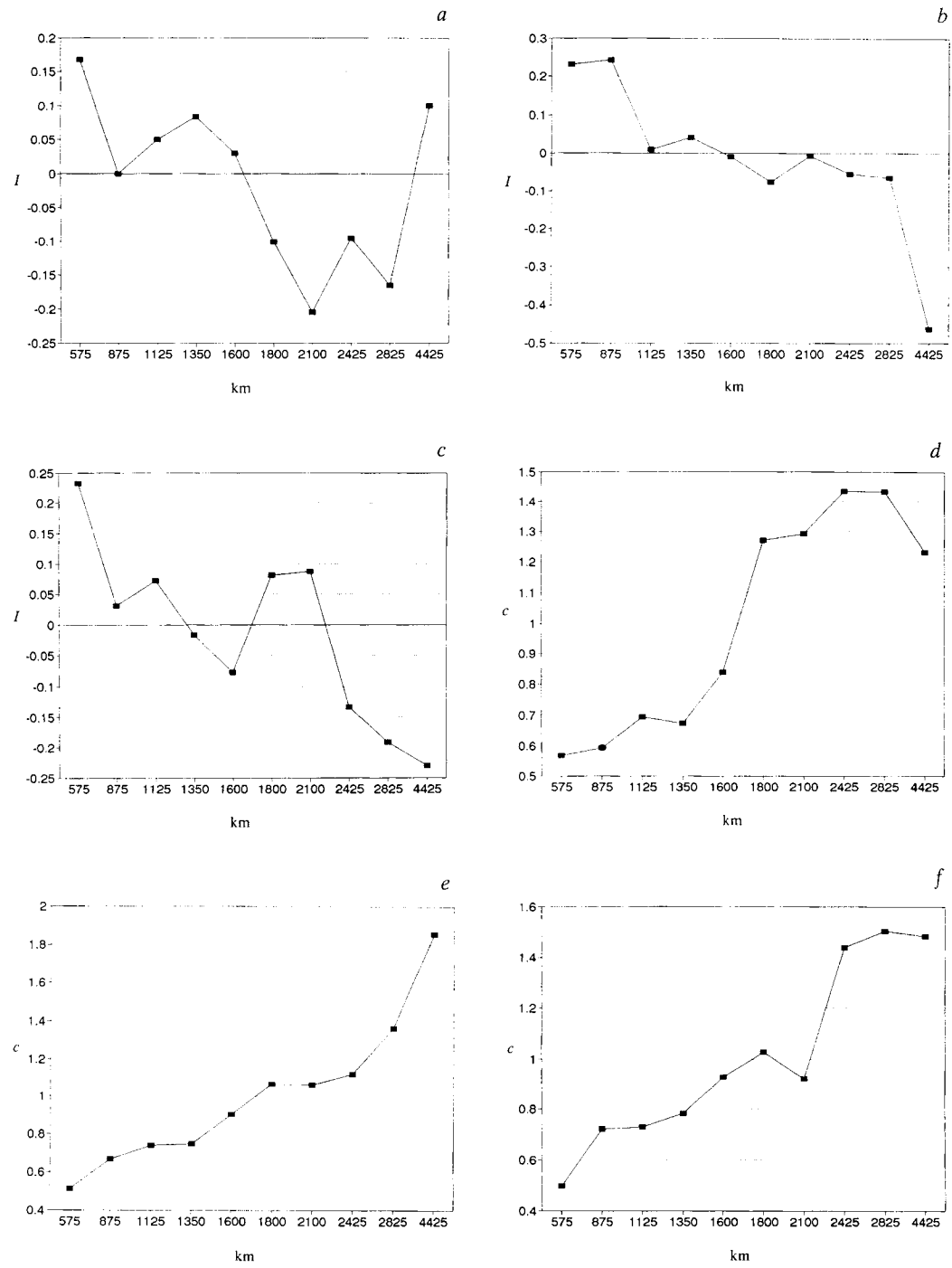


Fig. 2. Spatial correlograms for the scores of the first three factors. Ordinate: Moran's autocorrelation coefficient *I* or Geary's autocorrelation coefficient *c*, as indicated. Abscissa: Distance classes representing upper limits in km as indicated. **a:** Factor 1, *I*. **b:** Factor 2, *I*. **c:** Factor 3, *I*. **d:** Factor 1, *c*. **e:** Factor 2, *c*. **f:** Factor 3, *c*.

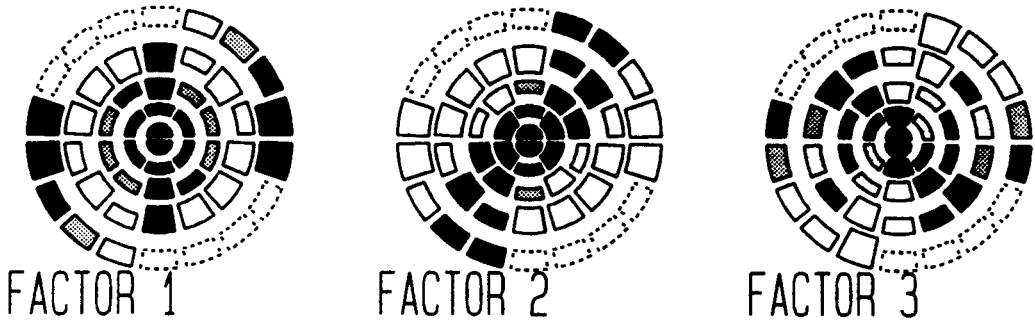
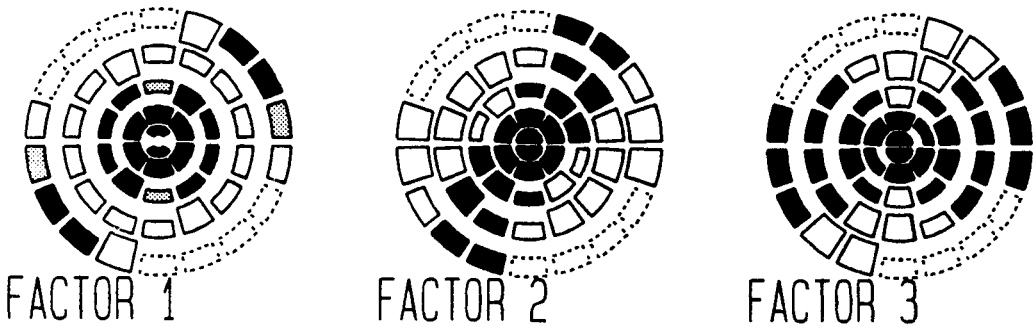
a*b*

Fig. 3. Directional spatial correlograms for the scores of the first three factors. The annuli represent distance classes with upper limits of 220, 780, 1,680, 2,920, and 4,500 km. The shading represents approximate quintiles of all autocorrelation coefficients as follows. *I*: no shading -2.0802 to -0.0952 ; light gray -0.0943 to -0.0337 ; medium gray -0.0320 to 0.0131 ; dark gray 0.0136 to 0.0697 ; black 0.0709 to 0.6870 . *c*:

No shading 0.3067 to 0.7577 ; light gray 0.7606 to 0.9170 ; medium gray 0.9192 to 1.0252 ; dark gray 1.0265 to 1.2233 ; black 1.2293 to 4.7975 . Statistically significant sectors ($P \leq .05$) are shown in full; nonsignificant ones are shown as narrower strips. Dotted sectors have an inadequate number of observations for evaluation. For an interpretation of the diagram, see text. *a*: *I*-Correlograms. *b*: *c*-Correlograms.

main-line terminations. The first three factors comprise exclusively finger patterns or finger ridge-counts and together account for almost 25% of the variance. Factors involving specific digits, such as 12, 14, and 15, also appear. Palm patterns and main-line terminations load on the same factors when the main-lines are involved in the formation of the patterns (e.g., factors 4 and 5). Certain

factors, most notably 17, 18, and 19, are poorly defined. Factors 17 and 19 consist of unilateral loadings on digit II radial loops, while 18 includes the odd combination of female left C-7 and male left B-6 terminations. Overall, these 20 factors provide a comprehensive description of finger and palm dermatoglyphic variability.

Next we examine the one-dimensional cor-

TABLE 1. Description of 20 factors used in the analysis¹

Factor No.	Factor description
1. 34.8%	Male ulnar ridge counts, whorl patterns, radial ridge counts (+); ulnar loops (-)
2. 18.5%	Female whorl patterns, ulnar and radial ridge counts (+); ulnar loops, arches (-)
3. 15.1%	Male and female radial ridge counts (+); arch patterns (-)
4. 12.6%	Female interdigital IV loops, interdigital III open fields, C-line ending in 5', B-line ending in 5, D-line ending in 7 and 9 (+); open fields in interdigital IV, loops in interdigital III, D-line ending in 11 (-)
5. 11.4%	Male, same loadings as No. 4, above
6. 10.3%	Male and female palmar interdigital ridge counts (+)
7. 8.3%	Male interdigital III loops, C-line ending in 9, interdigital IV loops with accessory triradius (+); interdigital III open fields, C-X endings (-)
8. 8.1%	Female axial triradius t, hypothenar open fields (+); axial triradius t' (-)
9. 7.2%	Male and female A-line endings in 1 and 3 (+); A-line ending in 4 (-)
10. 6.6%	Male, same loadings as No. 8 above
11. 5.9%	Male and female thenar open fields (+)
12. 4.9%	Female whorl patterns and ulnar ridge counts on digit I (+); ulnar loops on digit I (-)
13. 4.5%	Male and female B-line 5', A-line 4 (+); A-line 5' (-)
14. 4.3%	Male whorl pattern on digit V (+); ulnar loop patterns on digit V (-)
15. 4.2%	Female arches on digit II and V (+); radial loops on digit II (-)
16. 4.1%	Female interdigital III loops, C-line ending in 9 (+); interdigital III open fields (-)
17. 3.8%	Female radial loops on right digit II (+)
18. 3.7%	Female left C-line ending in 7 (+); male left B-line ending in 6 (-)
19. 3.4%	Male radial loop on left digit II (+)
20. 3.2%	Male arch patterns on digits III and IV

¹ Percent of covariation explained is followed by variables affecting factors positively (+) and negatively (-).

relograms for the 20 sets of factor scores. We adopt the conservative criterion of calling a factor significantly spatially autocorrelated only when the Bonferroni tests reject the null hypothesis of no spatial autocorrelation for both Moran's *I* and Geary's *c*. Only factors 1, 2, and 3 are significantly spatially autocorrelated by that criterion, and only three other factors would have been significant if we had admitted significance for just one spatial autocorrelation statistic. This is an unusually low proportion of autocorrelated surfaces when compared with other studies of Europeans.

We show the correlograms of the first three factors in Figure 2. The *I*-correlograms of factors 1 and 3 hint at clines, with significant spatial autocorrelation at the first distance class up to 575 km, and significant negative autocorrelation at 2,100 km and 2,825 km for factor 1 and above 2,100 km for factor 3. These are suggestions of clines, but they are not clearly expressed. The *c*-correlograms for these two factors show clearer clinal trends. The *I*-correlogram of factor 2 exhibits a good cline, and its *c*-correlogram manifests an even better one.

We illustrate the results of directional correlogram analysis in Figure 3 for the first three factors. These "windrose" diagrams show the extent of spatial autocorrelation by

the intensity of shading: from strong negative autocorrelation, unshaded, to strong positive autocorrelation, black. The successive rings, or annuli, of the diagram represent increasing geographic distance classes as indicated in the legends. A typical cline shows black at the center (positive autocorrelation at proximal geographic distances) and white at the periphery (negative autocorrelation at far distances), with shades of gray in between. The dark sectors are frequently in the shape of a "propeller." The axis perpendicular to the propeller gives the compass direction of the cline.

As *I*-correlograms the patterns for factors 1 and 3 are not at all clear, except for significant positive spatial autocorrelation at the first distance class (innermost ring in Fig. 3a) which corresponds to an upper limit of 220 kilometers. Factor 2 suggests a NW-SE cline through its propeller of high values positioned at right angles to that direction. In the *c*-correlograms (Fig. 3b), similar conditions obtain, but factor 3 also suggests a cline in an approximate north-south direction. Bonferroni tests had shown factors 1-3 to be significant, which matched our results for the one-dimensional autocorrelation analysis. Additionally there were two factors, significant in directional autocorrelation, that were not significant in one-dimensional au-

to correlation analysis; these are factors 11 and 17. Examination of the two-dimensional correlograms and of our computational results revealed that these factors are Bonferroni significant because of a single highly significant distance-direction class, unlike factors 1–3, which are significant because of several such classes. We therefore focus on an interpretation of factors 1, 2, and 3.

The interpolated surfaces for the three factors are shown in Figure 4. Factor 2, which has the clearest pattern, shows a trend affecting female finger pattern whorls and female finger ridge counts both positively. Finger pattern ulnar frequencies and arch frequencies are affected negatively. The trend extends from high values of the factor scores in the SE to low values in the NW, with highest values in the Crimea and in easternmost Europe abutting Siberia, with low values in Scandinavia and the British Isles, and with lowest values in the Faeroes and Iceland. The corresponding factor affecting the same variables in males is factor 1. It affects male finger patterns positively, and the ulnar loop frequencies of the finger patterns negatively. An examination of the interpolated map for this factor shows a general tendency paralleling that of factor 2, but this trend cannot be shown clearly and is not corroborated by the directional correlogram. Finally, factor 3, affecting male and female radial ridge counts (positively) and arch patterns (negatively), has low values in northern Europe, particularly among the Lapp populations of the Komi peninsula and high values along the Mediterranean, but the trend is none too clear and was substantiated only by the directional *c*-correlogram.

We ordinated the 74 localities for the first three factors, and in Figure 5 we show the results of the ordination of factor 1 against factor 2 as typical of the other ordinations attempted. Generally there is a large, undifferentiated central mass of populations, with outliers in various directions representing the Lapps, Udmurts, Tatars, Danes, Faeroese, and Icelanders. Thus we can see that some localities are clearly different from others; however, the mass of the localities is relatively undifferentiated, and we do not find regions of homogenous populations oc-

cupying different orthants of the ordinated space.

DISCUSSION

We have already enumerated the five categories into which the 236 variables fall. These categories are the same for each sex. Note that high loadings, and hence correlations, occur only between variables within one of these categories, so that the responses in most cases are restricted to a given category of characters. There are only two exceptions to this finding: most notably finger pattern types and finger ridge-counts and secondarily palm patterns and palm mainlines. Finger ridge-counts and finger patterns involve quantification and classification of patterns so must partly reflect the same source of variation, hence the high correlation. Certain palm patterns, primarily loops in interdigital areas III and IV, are often formed by recurvature of main-lines C or D, resulting in correlation for structural reasons. There appear to be no developmental factors causing high correlations between variables in different sets. In a study of correlation of distance matrices estimated from different categories of dermatoglyphic variables, Jantz et al. (1992) found that most categories correlated only at a low level with other categories, but that finger patterns and finger counts were highly correlated, and palm patterns and mainline terminations were moderately correlated. Our present findings confirm these earlier results.

To demonstrate migration, data analysts look for parallel variation patterns in a variety of genetic loci or morphological variables. Here there is no good evidence for migration patterns, since the only parallel patterns are generally within the same, correlated category of variables. Nevertheless, there is one good cline exhibited by factor 2. It is a NW-SE cline and as such supports the demic diffusion hypothesis of the origin of agriculture (Ammerman and Cavalli-Sforza, 1984; Sokal et al., 1991). In this respect it behaves like allele frequencies (Sokal et al., 1991) but unlike craniometric data (Harding et al., 1990).

The results of this study are notable for two unusual findings: All variables are significantly heterogeneous among localities,

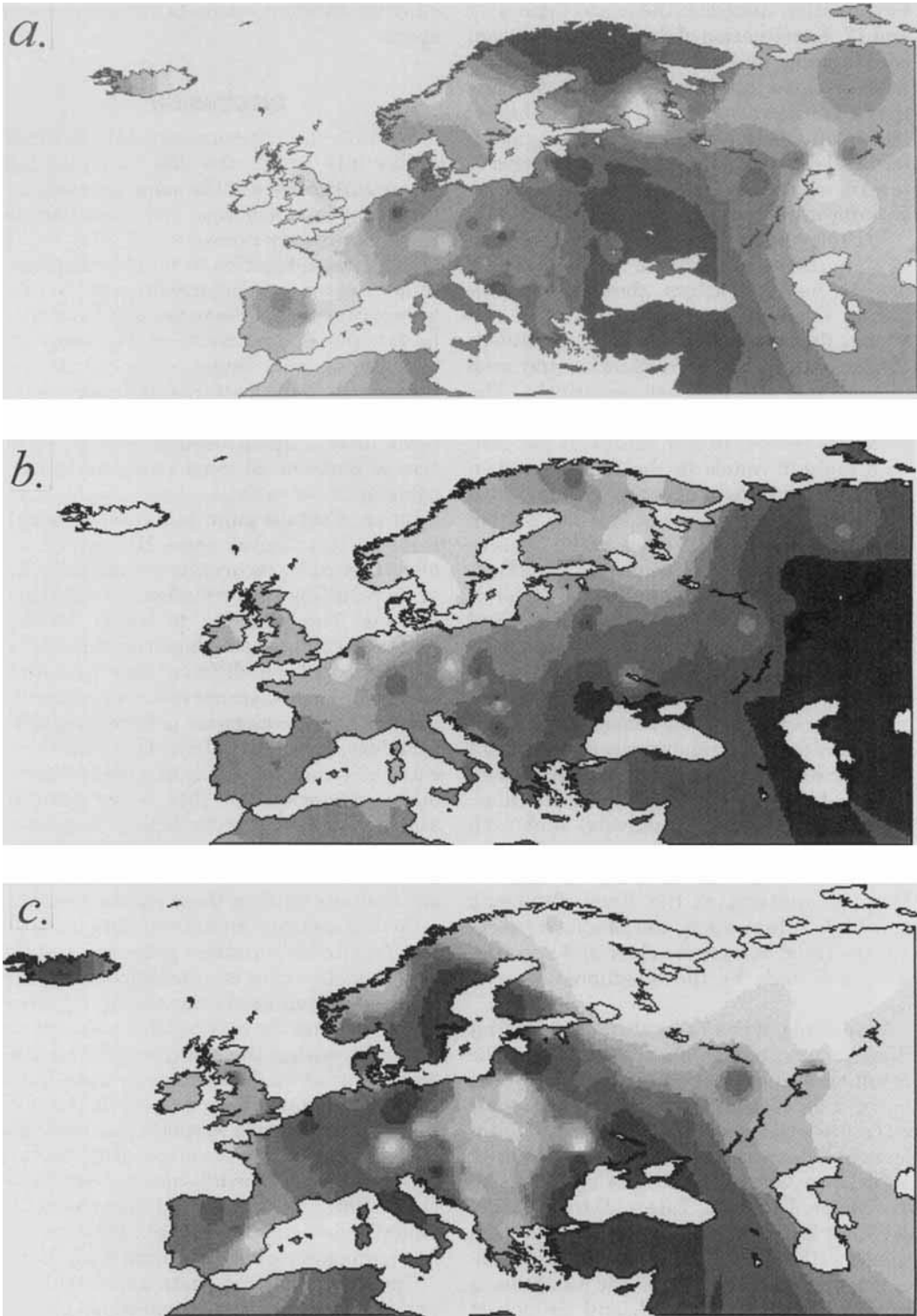


Fig. 4. Contour maps for scores of the first three factors. Intensity of the shading indicates the magnitude of the factor scores. The range of variation is divided into eight equal frequency classes. **a:** Factor 1. **b:** Factor 2. **c:** Factor 3.

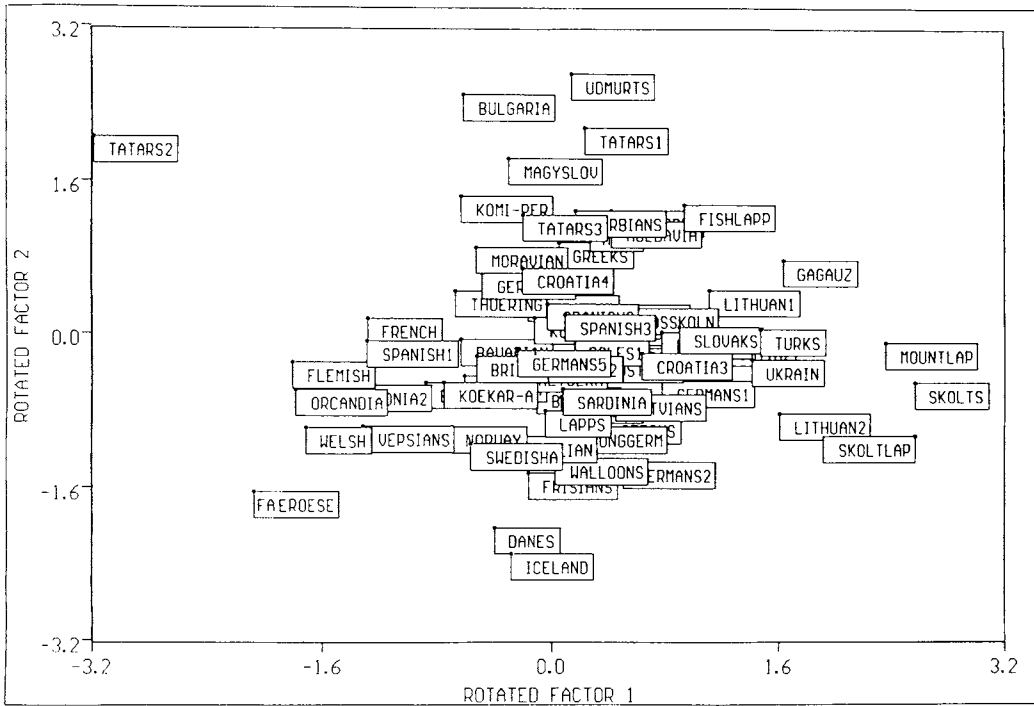


Fig. 5. The 74 localities ordinated for factors 1 and 2.

but there is very little significant spatial structure among the localities. From our knowledge of the biology of these populations, it is obvious that they could not be panmictic, and this inference is strongly supported by the significant heterogeneity among localities. But these data are also unique in having significant spatial structure in only three of the 20 extracted principal axes. In this respect the data are quite different from previous analyses of the populations of Europe based on craniometric variables (Sokal and Uytterschaut, 1987) and allele frequencies (Sokal et al., 1989). Not only is there but a single clear clinal trend in these data, but there are no significant short-distance autocorrelation coefficients indicating evidence for isolation by distance. The lack of spatial structure in these dermatoglyphic variables is paralleled in findings on 18 villages in Bougainville (Sokal and Friedlaender, 1982) that dermatoglyphic variables are less spatially structured at shorter geographical distances than anthropometric or dentometric variables or blood

polymorphisms. Both sets of findings suggest that dermatoglyphics can show spatial structure only over greater spatial distances than genetics and anthropometrics.

Closer examination of the factor scores reveals that for most factors there is considerable concentration of values near the middle of the sample distribution and that there are only a few outliers. As we have seen, these outliers include Tatars, Faeroese, Lapps, Icelanders, Orkney Islanders, Åland Islanders, and various West Finnic populations. Most outlier populations are non-Indo-European speakers, and/or small hence subject to drift, and/or have moved from elsewhere where they may have had a very different ancestry and genetic composition. But these populations are not necessarily geographical outliers, so it may be that no clear spatial patterns can be ascertained. For the bulk of the localities there may not be substantial local differentiation, so that the significant analyses of variance and heterogeneity *G*-tests may reflect the influence of the phenetically, but not spatially, outlying locality sam-

ples. Thus there may not be all that much local differentiation among localities except for the outliers, and the significant F and G values may reflect the presence of these outliers. Since the phenetic outlier populations are found at various places on the map, some peripheral and others quite central, one cannot establish a relationship between geographic distance and phenetic differentiation. One would therefore expect a low phenetic distance–geographic distance correlation and no spatial autocorrelation in these data.

These conjectures are supported by Jantz et al. (1992) who found that the correlation of phenetic distances with geographic distances were generally low and not significant, with the highest correlation occurring for finger-ridge counts, the lowest with mainline terminations and palm-ridge counts. If there are no correlations between phenetic and geographic distances, one would not expect spatial autocorrelation to be large or significant. This is exactly what we find. Again, the finger patterns and finger-ridge counts have the highest spatial autocorrelation, and those factors loading on palm patterns, mainline termination, and palm ridge counts have the lowest.

An intriguing aspect of these data is the lack of short-distance autocorrelation. Its presence would indicate local differentiation of populations with respect to dermatoglyphic variables. There are numerous (270) point pairs in the first distance class, so absence of significant spatial autocorrelation is not a function of too few nearby localities. The absence of local differentiation is puzzling when blood polymorphisms, as well as craniometric data, show local differentiation strongly and significantly. We should point out that in the study of blood polymorphisms (Sokal et al., 1989), ten of the 59 frequencies also had no discernible spatial pattern, so the dermatoglyphic data are not unique in lacking local spatial structure. We conclude that there is no evidence of local differentiation and no evidence for migration patterns or adaptive patterns.

When this study is compared with that of Sokal and Livshits (1993) based on six summary dermatoglyphic variables as defined by Heet (1983), we note that these showed highly significant spatial patterns

over the Eurasian continent. Five of the six variables were palm variables, while in the present study the variables are more evenly divided between fingers and palms. In this study only finger variables exhibited significant spatial patterning, while in the Sokal and Livshits study, finger pattern intensity and four of five palmar variables were significantly patterned. There were areas of low finger pattern intensity in Northwestern Europe, and higher pattern intensities in Southeastern Europe. This trend is reflected in our factor 2, and to a lesser extent in factors 1 and 3. Our results also confirm the earlier findings of Binkley (1985) who found significant spatial patterning in finger ridge-counts. Some of the palm variables in Sokal and Livshits (1993) find counterparts in our factors and some do not. Our factors 8 and 10 combine distal triradius t and hypothenar open fields. Hypothenar patterns and distal triradius t are treated as separate variables in Sokal and Livshits, but intercorrelation is implied by their combination into a factor. Thenar/I patterns are expressed in our factor 11 as thenar/I open fields, the complement of patterns. AIT, frequency of accessory interdigital triradii, is not expressed in our factors. Several of our factors express mainline endings, but none combines lines A and D as is done in the construction of the mainline index.

Sokal and Livshits' (1993) finding of significant spatial patterning in palm variables and its absence in the present study may be related to the lower heritabilities of palm patterns and to the more circumscribed area considered in the present study. Less is known about the heritability of palm patterns than of finger ridge-counts, partly because the former are categorical variables; hence their heritabilities are more difficult to estimate. Loesch and Swiatkowska (1977) report heritabilities for numbers of palm loops estimated from both twins and families. The heritabilities are highly variable, ranging from 0.10 to 0.73, but most cluster around 0.5. By contrast, finger ridge-counts on individual digits exhibit heritabilities ranging from 0.44 to 0.90, but most are over 0.7 (Loesch, 1983). These lower palm heritabilities may require larger geographic areas to reflect genetic variation. One observes from the contour plots in Sokal and Livshits

that large areas of Europe are homogeneous for certain traits, most prominently hypothenar patterns. The correlograms indicate that negative autocorrelation does not appear until 4,000–6,000 km, as opposed to 1,200–2,000 km for most genetic markers and craniometric traits (Sokal et al., 1989; Harding, 1990).

Finally, we can examine the ordination of the samples and compare it with published ordinations of European samples based on other sets of variables. Since unfortunately the identities of the samples do not correspond in the various studies, only some partial comparisons can be made, based mostly on outliers. The study by Derish and Sokal (1988) was based on 5×5 degree quadrats and featured both cranial and gene-frequency data (Figs. 4 and 5 in that study). The gene-frequency data have quadrats in northern Finland (presumably Lapps) and in Sardinia opposing each other along axis 1, and quadrats in Greece and Ireland opposing each other along axis 2. The cranial data show no marked outliers. A more detailed study of the cranial data by Sokal et al. (1987; Fig. 4) shows Tatars and Greeks versus Sardinians, and Russians from Kazan versus Bretons as outliers for the first two axes. The "principal-component map" (actually principal-coordinates ordination) based on gene-frequency data and shown as Figure 5.5.2 in Cavalli-Sforza et al. (1994) displays Lapps versus Basques, and Sardinians and Greeks versus Irish, Icelanders, and Norwegians as outliers on axes 1 and 2. The dermatoglyphic data of the present study (Fig. 5) feature Lapps versus Tatars, and Udmurts versus Icelanders, Danes, and Faeroese for the first two axes. It would appear that none of these groups are outliers for all the classes of variables examined, but that Lapps and Icelanders are outliers with respect to both genetics and dermatoglyphics. Tatars are outliers for craniometrics and dermatoglyphics, whereas Sardinians are outliers for craniometrics and genetics. Surprisingly, Basques, strong outliers in genetic studies (Cavalli-Sforza et al., 1994), do not stand out by either craniometrics or dermatoglyphics. In this study, Basques assume extreme values only for the sixth factor, which reflects their high palmar interdigital ridge counts. The Sardinians, extreme with respect to ge-

netics and craniometrics, are altogether unremarkable in their finger-print patterns. The data from all three classes of variables in our studies are consistent in presenting most European populations as a central undifferentiated cluster.

It is often assumed that dermatoglyphics are more suitable than most quantitative traits for analysis of human variation. Results are actually variable, presumably because of the extreme methodological variation one sees in dermatoglyphic research (Meier, 1980). The large number of variables and samples in the present study provides the most comprehensive assessment available to date. Our finding that finger patterns and ridge-counts exhibit spatial patterns similar to those found for blood markers supports the notion that dermatoglyphics reflect the major factors responsible for structuring human genetic variation in Europe. However, the absence of spatial structure in palm variables seems to indicate that palm variables are less useful and that they do not reflect the genetic structure of European populations. Jantz et al. (1992) have noted in a more limited context that palm distances have a relatively low correlation with finger distances. These findings suggest that our current understanding of what variation in palmar dermatoglyphic variables means is still very limited.

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LITERATURE CITED

Ammerman AJ, and Cavilli-Sforza LL (1984) *The Neolithic Transition and the Genetics of Populations in Europe*. Princeton, NJ: Princeton University Press.

Binkley KM (1985) *A search for systematic variability in inter-finger ridge count variation*. Ph.D. Dissertation, University of Tennessee, Knoxville.

Cavalli-Sforza LL, Menozzi P, and Piazza A (1994) *The History and Geography of Human Genes*. Princeton, NJ: Princeton University Press.

Cliff AD, and Ord JK (1981) *Spatial Processes*. London: Pion.

Derish PA, and Sokal RR (1988) *A classification of European populations based on gene frequencies and cranial measurements: a map-quadrat approach*. *Hum. Biol.* 60:801-824.

Harding RM (1990) *Modern European cranial variables and blood polymorphisms show comparable spatial patterns*. *Hum. Biol.* 62:733-745.

Harding RM, Rösing FW, and Sokal RR (1990) *Cranial measurements do not support Neolithization of Europe by demic expansion*. *Homo* 40:45-58.

Heet HL (1983) *Dermatoglyphics of the USSR peoples*. Moscow: Nauka (in Russian).

Jantz RL, Brehme H, and Eriksson AW (1992) *Dermatoglyphic variation among Finno-Ugric speaking populations: methodological alternatives*. *Am. J. Phys. Anthropol.* 89:1-10.

Loesch DZ (1983) *Quantitative Dermatoglyphics. Classification, Genetics and Pathology*. New York: Oxford University Press.

Loesch D, and Swiatkowska Z (1977) *Topologically significant dermatoglyphic patterns in twins*. *Acta Genet. Med. Gemollo. (Roma)* 26:247-258.

Meier RJ (1980) *Anthropological dermatoglyphics: a review*. *Yrbk. Phys. Anthropol.* 23:147-178.

Oden NL (1984) *Assessing the significance of a spatial correlogram*. *Geogr. Ana.* 16:1-16.

Oden NL, and Sokal RR (1986) *Directional autocorrelation: an extension of spatial correlograms to two dimensions*. *Syst. Zool.* 35:606-617.

Sneath PHA, and Sokal RR (1973) *Numerical Taxonomy*. San Francisco: W.H. Freeman.

Sokal RR (1979) *Ecological parameters inferred from spatial correlograms*. In SP Patil and ML Rosenzweig (eds): *Contemporary Quantitative Ecology and Related Ecometrics*. Fairland, MD: International Co-operative Publishing House, pp. 167-196.

Sokal RR (1984) *Spatial analysis in population biology and regional science*. In ÅE Andersson, W Isard, and T Puu (eds): *Regional and Industrial Development Theories, Models, and Empirical Evidence*. Amsterdam: Elsevier Science Publishers B.V. (North-Holland), pp. 241-266.

Sokal RR (1986) *Spatial data analysis and historical processes*. In E Diday, Y Escoufier, L Lebart, J Pages Y Schektman, and R Tomassone (eds): *Data Analysis and Informatics, Vol IV*. Amsterdam: Elsevier Science Publishers B.V. (North-Holland), pp. 29-43.

Sokal RR, and Friedlaender J (1982) *Spatial autocorrelation analysis of biological variation on Bougainville Island*. In MH Crawford and JH Mielke (eds): *Current Developments in Anthropological Genetics, Vol. 2*. New York: Plenum, pp. 205-227.

Sokal RR, and Livshits G (1993) *Geographic variation of six dermatoglyphic traits in Eurasia*. *Am. J. Phys. Anthropol.* 90:393-407.

Sokal RR, and Oden NL (1978a) *Spatial autocorrelation in biology 1. Methodology*. *Biol. J. Linn. Soc.* 10: 199-228.

Sokal RR, and Oden NL (1978b) *Spatial autocorrelation in biology 2. Some biological implications and four applications of evolutionary and ecological interest*. *Biol. J. Linn. Soc.* 10:199-228.

Sokal RR, and Rohlf FJ (1995) *Biometry*, 3rd ed. New York: W.H. Freeman.

Sokal RR, and Uytterschaut H (1987) *Cranial variation in European populations: a spatial autocorrelation study at 3 time periods*. *Am. J. Phys. Anthropol.* 74:21-38.

Sokal RR, and Wartenberg DE (1981) *Space and population structure*. In D Griffith and R McKinnon (eds): *Dynamic Spatial Models*. The Netherlands: Sijthoff and Noordhoff, Alphen aan den Rijn, pp. 186-213.

Sokal RR, Harding RM, and Oden NL (1989) *Spatial patterns of human gene frequencies in Europe*. *Am. J. Phys. Anthropol.* 80:267-294.

Sokal RR, Oden NL, and Wilson C (1991) *Genetic evidence for the spread of agriculture in Europe by demic diffusion*. *Nature* 351:143-145.

Sokal RR, Uytterschaut H, Rösing FW, and Schwidetzky I (1987) *A classification of European skulls from three time periods*. *Am. J. Phys. Anthropol.* 74:1-20.

Späth H (1980) *Cluster Analysis. Algorithms for Data Reduction and Classification of Objects*. Chichester, UK: Ellis Horwood.

Upton GJG, and Fingleton B (1985) *Spatial Data Analysis by Example, Vol. I. Point Pattern and Quantitative Data*. Chichester, England: John Wiley.

APPENDIX A. Details of location, size, and source of samples used in this study¹

Group	Location	Sample Sizes		LAT	LONG	Investigators
		♂	♀			
Austrians	Vienna, Austria	520	520	48.13N	16.22E	Hauser, G.
Baltic Germans	Russian SFSR	66	47	55.00N	22.30E	Ehrhardt, S.
Basques	Vizcaya Province, Spain	136	113	43.20N	2.45W	Arrieta, I.
Bavarians	Munich, Germany	91	91	48.08N	11.34E	Schwarzfischer, F.
Bretons	Concarneau, Plouhine, France	117	120	47.52N	3.55W	Jakobi, L.
British	Lake District, England	273	273	54.30N	3.10W	Roberts, D. F.
Bulgarians	Moldavian SSR	66	66	47.00N	29.00E	Dolinova, N.
Byelorussians	Vitebsk & Minsk, Byelorussia	72	72	54.30N	28.00E	Heet, H.

APPENDIX A. (cont'd) Details of location, size, and source of samples used in this study¹

Group	Location	Sample Sizes		LAT	LONG	Investigators
		♂	♀			
Cornish	Cornwall, England	106	144	50.30N	4.40W	Harvey, R.
Croatians	Zagreb, Croatia	103	102	45.48N	15.58E	Skrinjaric I.
Croatians	Katymar, S. Hungary	93	90	46.06N	18.16E	Gyenis, G.
Croatians	Korcula Island, Croatia	120	120	42.58N	17.08E	Milicic, J.
Croatians	Baranya Co., S. Hungary	94	82	46.05N	18.15E	Hera, G.
Czechs	Prague, Czech Republic	130	110	50.05N	14.26E	Kuklik, M. & Copova, M.
Danes	Copenhagen, Denmark	103	71	55.40N	12.35E	Palsson, J.
Dutch	Heerlen & Utrecht, Netherlands	110	111	51.26N	5.30E	Bringmann, B. J. G.
Estonians	Haapsalu, Estonia	76	62	58.56N	23.33E	Heet, H.
Estonians	Schwaebisch Hall, Germany	134	108	59.00N	26.00E	Ehrhardt, et al.
Faeroese	Faeroe Islands	135	160	62.00N	7.00W	Harvey, R.
Finns, North	Oulu, Finland	248	270	65.00N	25.26E	Forsius, H. et al.
Fisher Lapps	Inari, Finland	52	63	68.54N	27.01E	Juergens, H. & Lehmann, W.
Flemish	Oostende, Belgium	72	93	51.13N	2.55E	Vrydagh, S. et al.
French	Ville Arthez D'Asson, France	90	101	43.15N	0.50W	Jakobi, L.
Frisians	East Friesland, Germany	66	51	53.20N	7.40E	Schade, H.
Gagauz	Moldavian SSR	60	60	47.01N	29.00E	Dolinova, N.
Germans	Kiel, Germany	111	108	54.20N	10.08E	Juergens, H. et al.
Germans	Berlin, Germany	210	350	52.32N	13.25E	Brehme, H.
Germans	Duesseldorf, Germany	94	105	51.14N	6.47E	Schade, H. & Scheil, H.-G.
Germans	Leipzig, Germany	108	79	51.19N	12.20E	Brehme, H.
Germans	Wuerttemberg, Germany	74	89	48.32N	9.04E	Ehrhardt, S.
Greeks	Thessaloniki, Greece	176	155	40.38N	22.57E	Pentzos-Daponte
Hungarians	Domsod, Hungary	132	138	47.00N	19.03E	Gyenis, G.
Germans	Hajos, Hungary	105	131	46.24N	19.07E	Gyenis, G.
Icelanders	Reykjavik, Iceland	93	98	64.09N	21.51W	Palsson, J.
Italians	Rome, Italy	55	104	41.53N	12.30E	Fuciarelli, M.
Karelians	Karelian ASSR	73	72	62.30N	32.35E	Heet, H. & Dolinova, N.
Koekars	Mariehamn, Aland Is.	40	44	60.06N	19.57E	Brehme, H. & Eriksson, A.
Komi-Permyak	N. Permian District, Russia	59	60	58.00N	50.15E	Dolinova, N.
Komi-Zyrians	Komi ASSR	72	74	63.31N	53.15E	Dolinova, N.
Lapps	Kola Peninsula, Russia	72	74	68.58N	33.05E	Heet, H.
Latvians	Schwaebisch Gmuend, Germany	182	152	57.00N	25.00E	Valunas
Lithuanians	Schwaebisch Hall, Germany	116	87	56.00N	24.00E	Erhardt, S.
Lithuanians	Telschaj, Lithuania	67	95	56.01N	24.01E	Heet, H.
Magyar-Slovaks	Domoszló, Hungary	86	79	47.00N	19.00E	Gyenis, G.
Mari	Mari ASSR	72	84	56.20N	48.00E	Dolinova, N.
Moldavians	Moldavian SSR	54	54	47.00N	29.01E	Dolinova, N.
Moravians	Olomouc, Czech Rep.	100	100	49.39N	17.15E	Hajan, V.
Mordvians	Mordvinian ASSR	75	75	54.18N	43.50E	Dolinova, N.
Mountain Lapps	Inari, Finland	24	24	68.54N	27.00E	Juergens, H. & Lehmann, W.
Norwegians	Trondheim District, Norway	106	62	63.25N	10.25E	Palsson, J.
Orcadians	Mainland, Orkney Islands	322	323	59.01N	3.08W	Brothwell, D.
Poles	Cracow, Poland	136	116	50.03N	19.58E	Wojciechowska, H.
Poles	Augustow Distr., Poland	45	53	53.51N	22.59E	Pospisil, M.
Roskolniki	Augustow Distr., Poland	98	117	53.52N	23.00E	Ferak, V.
Russians	Novgorod, Kaluga, Russia	126	126	54.30N	29.11E	Heet, H. & Dolinova, N.
Sardinians	Sardinia, Italy	149	136	40.00N	9.00E	Floris, G. et al.
Serbians	Vojvodina, Serbia	99	97	44.00N	19.00E	Krstic, A.
Skolt	Nellim, Finland	41	41	68.55N	28.10E	Juergens, H. & Lehmann, W.
Skolt Lapps	Sevettijaarvi, Finland	55	69	69.26N	28.38E	Juergens, H. & Lehmann, W.
Slovaks	Myjava, Slovakia	181	155	48.45N	17.34E	Pospisil, M.
Spanish	Andalusia & Barcelona, Spain	110	95	39.30N	1.10W	Vrydagh, S. et al.
Spanish	La Alcarria, Spain	99	100	40.30N	2.45W	Portables, D.
Spanish	Tierra de Campos, Spain	99	101	42.10N	4.50W	Martin, J.
Swedes	Mariehamn, Aland Is.	78	72	60.07N	19.58E	Brehme, H. & Eriksson, A.
Tatars	Crimea, Ukraine	75	72	45.00N	34.00E	Heet, H.
Tatars	Khargaly, Tatar ASSR	20	41	55.21N	50.37E	OMSK UNIV. EXPED.
Tatars	Tatar ASSR	98	95	55.00N	51.00E	Dolinova, N.
Thuringians	Leipzig, Germany	64	47	51.20N	12.21E	Hammer, H.-J. et al.
Turks	Istanbul, Turkey	35	42	41.01N	28.58E	Atasu, M.
Udmurts	Udmurtia ASSR	84	80	57.00N	53.00E	Dolinova, N.
Ukrainians	Ukraine	72	72	49.00N	32.00E	Heet, H.
Vepsians	Karelian ASSR & St. Petersburg	72	72	62.00N	32.00E	Heet, H. & Dolinova, N.
Waloons	St. Ghislain, Belgium	102	138	50.27N	3.49E	Vrydagh, S. et al.
Welsh	Caerna, Anglesey Island	240	83	53.15N	4.22W	Fraser-Smith & Sunderland, E.

¹ Coordinates are given in degrees and minutes. In many instances colleagues who furnished data have published on these data themselves. Because the samples were reanalyzed by a common method, we do not provide the citation to the original articles. Our analysis results in different data, and in some cases larger samples have been subsampled due to missing data. The sample sizes shown here are maxima. Samples from the former Soviet Union were obtained prior to the recent political changes, so we have partly retained the original locality designations.